

**MATING IN THE ABSENCE OF VISUAL CUES BY
SCHIZOCOSA OCREATA (HENTZ 1844) WOLF
SPIDERS (ARANEAE, LYCOSIDAE)**

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ABSTRACT. Male *Schizocosa ocreata* (Hentz 1844) wolf spiders court females with multi-modal displays that include both seismic and visual components. The seismic components are thought to be ancestral whereas the visual components are thought to have been more recently derived. We here present evidence that, despite the evolution of elaborate visual display components in males, female *S. ocreata* remain able to derive sufficient information about males through the seismic display components alone. We compared the mating tendency of females courted by males in the light (seismic and visual components present) and in the dark (only seismic components present). With a sample of 79 pairs in each condition, pairs were not significantly less likely to mate when in the dark (62%) than when in the light (73%). While all males performed courtship, and latency from the release of males until the onset of courtship was similar in the light and in the dark, latency until mounting tended to be much longer in the dark. This may mean that it takes longer for females to gather the information required to accept a male in the absence of visual cues or may instead simply reflect the challenge of locating mates and orienting for mounting. Lighting conditions did not influence how long the male remained mounted, indicating that these wolf spiders lack the condition-dependent flexibility in copula duration that is found in some jumping spiders.

Keywords: Multimodal signalling, vision, Lycosidae

Spiders have provided valuable models for recent studies into the function and evolution of “multi-modal communication” (sensu Partan & Marler 1999). In particular, the wolf spider genus *Schizocosa* Chamberlin 1904 (Lycosidae) has been widely adopted as a productive model system. *Schizocosa* vary in their use of seismic and visual displays in courtship communication, ranging from stationary palpal stridulation with little detectable movement through to combinations of stridulation and percussion along with extravagant raising and waving of ornamented legs (Uetz 2000; Stratton 2005). Seismic signalling appears to be ancestral, and is used by all *Schizocosa* species regardless of whether they also have visual display components (Stratton 2005). On the other hand, dynamic and morphological visual signalling components are observed in only a subset of *Schizocosa* species and appear to have evolved more recently (McClintock & Uetz 1996; Hebets & Uetz 1999; Uetz 2000; Stratton 2005).

One of the key questions in studies of multi-modal communication is of the extent to which each modal component contributes to receiver responses. Recently, Hebets (2005) investigated the extent to which the male visual and seismic courtship components are required for female acceptance in *S. uetzi* Stratton 1997, a species with only rudimentary visual displays. During courtship, male *S. uetzi* stand stationary while stridulating with their pedipalps. Their forelegs have darkened mid-tibiae and, while stridulating, they intermittently raise their forelegs in a slow arch (Stratton 1997). Hebets (2005) found that pairs were similarly likely to mate in the dark (visual components occluded) as in the light (visual components present), as long as the seismic components were present. That is, the evolution of visual display components in this species appears not to have extinguished their ability to interact and make mating decisions when limited to the ancestral seismic components alone. Is this also the case in *Schi-*

zocosa species with more developed visual display components?

Compared with *S. uetzi*, *S. ocreata* (Hentz 1844) has much more elaborate dynamic visual elements in its courtship and more elaborate morphological modifications that are thought to enhance detection of signals (Uetz & Denterlein 1979; Stratton & Uetz 1981, 1983, 1986; Uetz 2000; Taylor et al. 2005). Two quite different seismic components are produced along with visual displays; percussion is produced by rapidly "jerking" the body downward to strike the substrate, and strong bursts of stridulation are produced by specialized organs in the pedipalps as the spiders display visually by moving their forelegs up and down. Males have dark forelegs bearing large tufts and in several studies females have shown greater receptivity toward males with large tufts (McClintock & Uetz 1996; Scheffer et al. 1996; Uetz 2000; Persons & Uetz 2005).

In this study, we investigate how often the seismic courtship component alone provides sufficient information for *S. ocreata* females to accept males as mates. From an evolutionary perspective, we are hence asking about the extent to which these spiders have come to depend on the secondarily added visual display components. If females are usually able to obtain all the information they need to accept males as mates even when the visual signalling component is altogether absent, we should find similar mating tendency in the light and in the dark. On the other hand, if the visual mode provides necessary information, we should find a marked reduction in mating tendency of pairs in the dark. In addition to considering the female's decision of whether to accept the male as a mate, we also consider other measures of male sexual success, including latency until mounting from the start of trials and from the onset of courtship, and how long the male remained mounted.

Sub-adult males and females of *S. ocreata* were collected from dense leaf litter at Cincinnati Nature Center, Rowe Woods (Clermont County, Ohio, USA: 39°07.556'N, 84°15.059'W), during March, April, May and September 2001. We kept spiders visually isolated from each other in white cylindrical plastic cages (11 cm diameter, 8.5 cm high) under laboratory conditions of 13:11 L:D photoperiod, ~23 °C and ~65% RH. Spiders were

fed 2–3 crickets twice weekly and had continual access to water by way of a soaked cotton wick inserted through a hole in the cage floor into a reservoir below. Spiders matured in the laboratory and were used in experiments between 7 and 50 days after maturing. All spiders were virgins when tested.

Mating trials were carried out in open plastic boxes (150 × 100 × 50 mm, lwh) during the laboratory light phase (which corresponded closely with daylight), excluding the first and last two hours. In nature, we have often seen *S. ocreata* courtship taking place in dark places (e.g., in dense leaf litter under forest canopy) during the day. Since all trials were run at the same period of the day, we controlled for possible biorhythms in the behavior of the spiders. A clean piece of 5 mm thick foam-core board covered the floor. This material allows excellent transmission of vibrations. A thin film of Vaseline® petroleum jelly prevented spiders from climbing out of the box. A new piece of foam-core board was used in each trial, and the plastic box was washed with warm soapy water and 70% ethanol between trials to remove any silk and chemical cues. All trials were carried out in a photographic darkroom. For trials in the light, illumination was provided by two 25 W fluorescent lights suspended 0.5 m above the arena (mean 87.8 ± SE 1.3 lx). For trials in the dark (no detectable visible light), illumination was provided by an Infra-Red (IR) light source (Sony HVL-IRC). Wolf spider eyes are not sensitive to IR light (DeVoe 1972, summarized in Yamashita 1985) and so this setup is equivalent to total darkness for the spiders. All trials were video-recorded using an IR-sensitive camera (Watec WAT-902C) positioned above the testing arena, which was connected to the video input of a VHS VCR (Sony DA Pro 4 head).

Virgin females were released into the arena 1 h before males. During this hour, males were kept in the light conditions under which the trial was to be carried out. Males were then transferred into the testing arena from maintenance cages by the use of a 10 ml plastic vial. Pairs were left to interact for two hours after which un-mounted pairs were returned to their home cages. Mounted pairs were video-recorded until they separated naturally. There were no incidences of sexual cannibalism either in the light or in the dark.

Effects of light regime on the probability of mating were investigated by log-likelihood ratio (G). Effects of light regime on latency from male release until onset of courtship, latency from male release until mounting, latency from onset of courtship until mounting, and how long the male was mounted (“mount duration”) were analyzed by Wilcoxon two-sample tests, using approximation to the normal distribution z (none of these data sets were normally distributed or of equal variance). All analyses were carried out using JMP v5 (SAS Institute).

With a sample size of 79 trials in each condition, pairs of *S. ocreata* wolf spiders were not significantly less likely to mate when in the dark (seismic display component only) than when in the light (visual + seismic display components available). Mounting and copulation was recorded within the 2-h testing period in 58 (73%) trials in the light and 49 (62%) trials in the dark ($n = 158$, $G_1 = 2.354$, $P = 0.125$). In previous studies, female *S. ocreata* have given “receptivity displays” to unseen courting males in adjacent chambers that occlude visual contact but allow transmission of seismic signals (Scheffer et al. 1996; Uetz 2000). Results of this study of direct interactions are consistent with results of these previous studies of female responses to males in adjacent chambers, indicating that female *S. ocreata* are usually able to obtain whatever information they need about a male through the seismic components of multimodal signals alone. Our results for *S. ocreata* are also very similar to those for *S. uetzi* by Hebets (2005), who found no evidence of reduced mating tendency when trials were run in darkness.

While choice of minor display elements and non-display behavior may vary slightly depending on whether *S. ocreata* males are courting in the dark or in the light, major display elements are performed similarly and the visual and seismic components of each display element are both retained regardless of lighting conditions (Taylor et al. 2005). The close synchrony of visual and seismic signaling components in *S. ocreata* means that display rates in these modes are tightly linked. In some wolf spiders, display rate is a key male attribute on which females base mating decisions (Kotiaho et al. 1996; Parri et al. 1997). If females of *S. ocreata* are also inter-

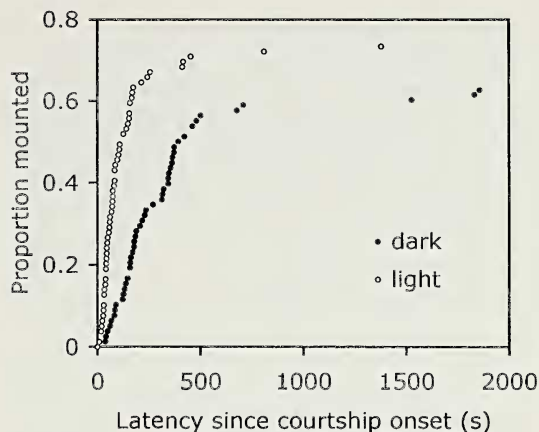


Figure 1.—Cumulative proportion of spiders mounted over time after the onset of courtship. The last spider to mount in the light was at 1378 s after the male began courting (1407 s after the male was released); the last in the dark was at 1857 s after the male began courting (1898 s after the male was released).

ested primarily in male display rate, then they may gain sufficient information regardless of whether the visual display components are present.

All tested males performed the major courtship element of “jerky tapping” (Stratton & Uetz 1981, 1983, 1986) during trials, regardless of whether they succeeded in mounting the female. Latency from release of the male until the onset of courtship did not vary between the dark (median = 22 s, range = 1–551 s) and in the light (median = 28 s, range = 2–415 s) ($n = 158$, $z = 0.030$, $P = 0.976$). However, latency from the onset of courtship until mounting was greater in the dark (median = 230 s, range 38–1857 s) than in the light (median = 74.5 s, range 9–1378 s) ($n = 107$, $z = 5.431$, $P < 0.001$; Fig 1). Similarly, latency from release of the male until mounting was greater in the dark (median = 308 s, range 42–1898 s) than in the light (median = 111 s, range 31–1407 s) ($n = 107$, $z = 5.271$, $P < 0.001$). One potential explanation for this is that females take longer over decisions to accept males when in the dark, needing more time to acquire critical information about their suitors. Alternatively, these differences in mounting latency may simply reflect the relative ease with which males can locate females, orient and mount or with which fe-

males can evade persistent males in the light and in the dark.

The duration of the period during which the male remained mounted on the female in this study was similar to durations reported in previous studies of *S. ocreata* and other *Schizocosa* species (Hebets et al. 1996; Stratton et al. 1996; Norton & Uetz 2005) and was similar in the dark (median = 159 min, range 45–608 min) and in the light (median = 144 min, range 70–719 min) ($n = 107$, $z = 0.372$, $P = 0.710$). In jumping spiders (Salticidae), males may remain mounted for longer when in the dark or in a secluded retreat where they are protected from visually orienting predators (Jackson 1980, 1992; Taylor & Jackson 1999). There are many visually orienting predators in the habitat where spiders were collected for this study, including pompilid wasps, birds, toads (pers. obs.) and conspecifics (Wagner & Wise 1996; Roberts et al. 2003). The similarity of mount duration in the light and in the dark for *S. ocreata* suggests that these spiders lack the apparent risk-dependent copulation tactics of jumping spiders.

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